

# A New Family of Poecilostomatoid Copepods (Umazuracolidae) Based on Specimens Parasitic on the Black Scraper (*Thamnaconus modestus*) in Japan

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*Umazuracola elongatus* n. gen., n. sp., is described based on specimens collected from the body surface of the black scraper, *Thamnaconus modestus* (Günther), taken from the Seto Inland Sea in western Japan. The new species belongs to a new family of the copepod order Poecilostomatoida. It is characterised by the reduction of the maxilliped and leg 1 in females and modification in both sexes of legs 2, 3, and 4 into robust attachment organs, with heavy, denticulate outer spines. Although the antenna, mandible, maxillule, and maxilla of *U. elongatus* resemble those of species of the “bomolochiform complex”, a cladistic analysis revealed that phylogenetically this species is embedded in a different clade containing the polychaete-parasitizing families Entobiidae Ho, 1984 and Nereicolidae Claus, 1875.

**Key words:** parasitic copepods, Poecilostomatoida, Umazuracolidae, black scraper

## INTRODUCTION

The copepod order Poecilostomatoida comprises mostly symbiotic members, with only a few species being planktonic (Ho, 1991; Huys and Boxshall, 1991). Recently, because of concern over inadequate knowledge of the phylogenetic relationships between the copepod orders Cyclopoida and Poecilostomatoida, Boxshall and Halsey (2004: p. 41) merged all families of Poecilostomatoida into the Cyclopoida. Traditionally, these orders have been clearly distinguished by (1) the number of segments on the antennule, (2) the structure of the maxillipeds of both sexes, (3) the location of female genital apertures, and (4) the presence or absence of geniculation in the male antennule. Therefore, we here retain the traditional concept of the Poecilostomatoida, which was established by Thorell (1859). Since cyclopoid classification is still in a state of flux, the arbitrary merging of poecilostomatoid families into Cyclopoida without rigorous phylogenetic support is not justified.

During our survey of parasitic copepods in East Asia, an undescribed species of the Poecilostomatoida was found parasitic on the body surface of black scrapers, *Thamnaconus modestus* (Günther), caught in the Seto Inland Sea of western Japan in August 2003 and May 2005. As far as we are aware, there is only one record of a previous species of poecilostomatoid copepod, *Taeniacanthus balistae* (Claus, 1864), parasitic on a fish of this species taken from the same

sea. Yamaguti and Yamasu (1959) and Shiino (1960) reported this parasite as “*Taeniacanthus longichela* Yamaguti and Yamasu, 1959” parasitic on “*Cantherhines modestus* (Günther).” A close examination of our new species indicated that it belongs to a new family of the Poecilostomatoida. In this paper, we report the results of a cladistic analysis conducted to determine the phylogenetic position of the new family, and we also describe the new species.

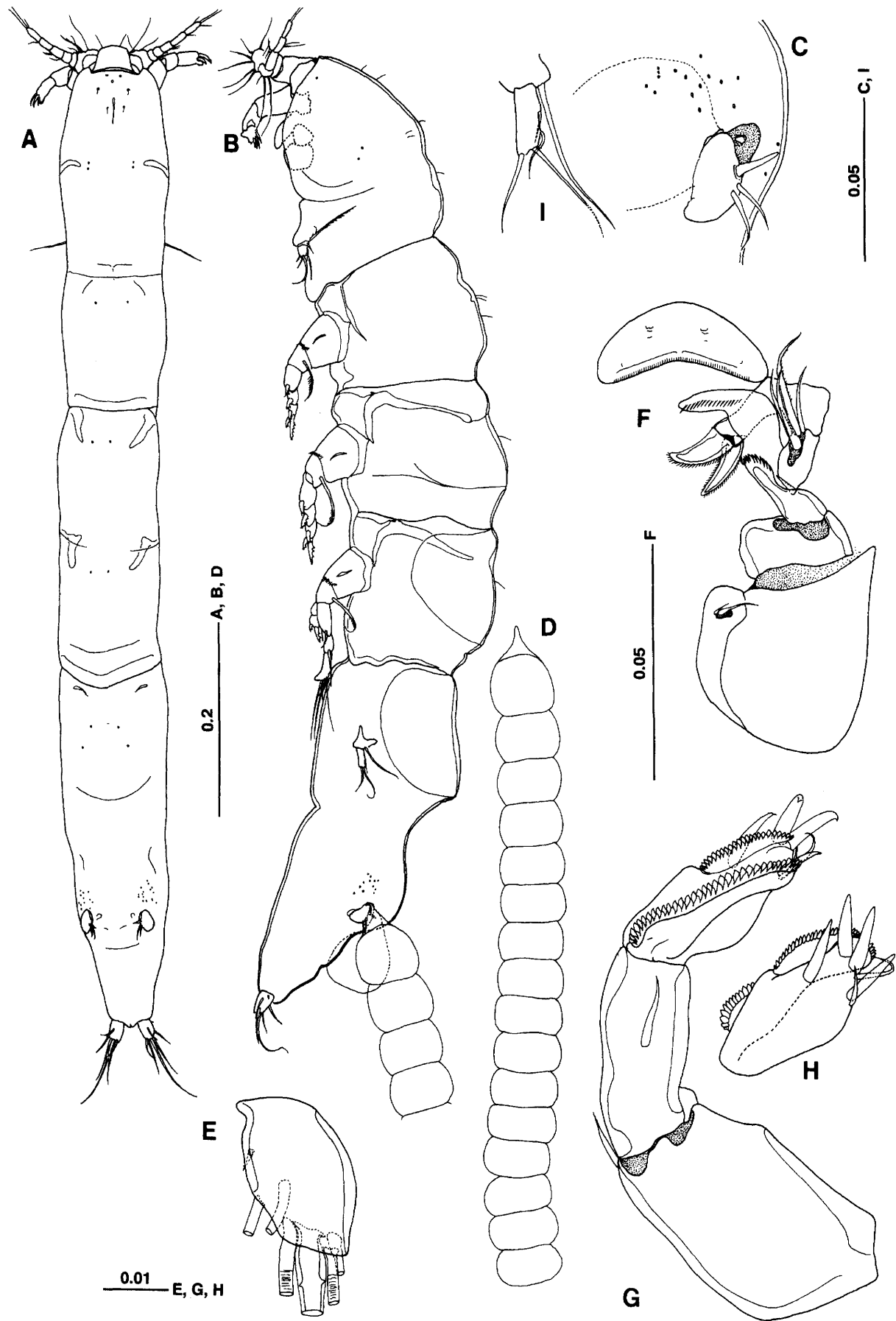
## MATERIALS AND METHODS

Copepod parasites were removed from the body surface of black scrapers (*Thamnaconus modestus*; total length 236–300 mm) and preserved in 70% ethanol. The specimens were later soaked in 85% lactic acid for a few hours before dissection under a stereoscopic microscope. Following the method of Humes and Gooding (1964), removed appendages and body parts were examined under a microscope with differential interference contrast (Nikon Optiphot). Two specimens collected on 1 August 2003 were dehydrated in alcohol-series, sputter-coated, and examined with a scanning electron microscope (Jeol T-20).

A cladistic analysis of the order Poecilostomatoida was conducted by Ho (1991) to determine the phylogenetic relationships among the 47 families then known. However, the order now comprises 61 families (Martin and Davis, 2001); thus, the cladistic analysis needed to be performed anew. In total, we utilized 138 morphological characters (Appendix 1) in a new analysis, all of them encoded in binary states. Our data matrix of the 138 characters and their states in the 61 poecilostome families is given in Appendix 2. As in Ho's (1991) previous analysis, the family Cyclopinidae was used as a outgroup. An unordered transformation of character states was also employed, to avoid an *a priori* predetermination of the topology of the resultant cladogram. The phylogenetic analysis was performed with HENNIG86 Version 1.5 software (Farris, 1988),

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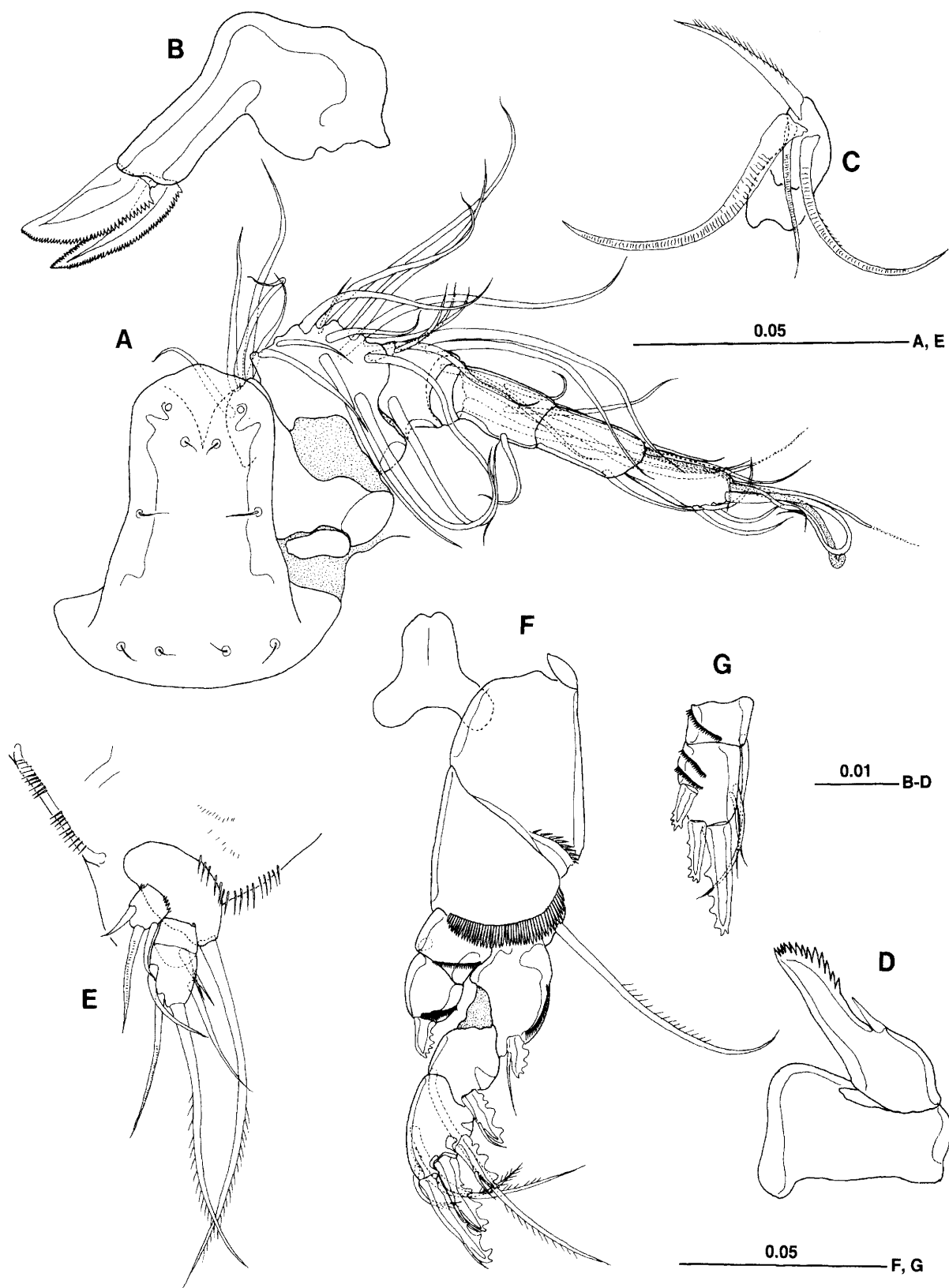


**Fig. 1.** *Umazuracola elongatus* n. g., n. sp., female (A, C, F–I, paratypes; B, D, E, holotype). **A**, habitus, dorsal. **B**, habitus, lateral. **C**, genital area and leg 6. **D**, egg sac. **E**, caudal ramus, ventral. **F**, labrum and oral appendages. **G**, antenna. **H**, endopod of antenna. **I**, leg 5, anterior. Scales in millimeters.

using the commands "mhennig" and "bb". The first command constructs several initial trees and saves only one shortest tree after limited branch-swapping; the second performs extended branch swapping on this initial cladogram to produce multiple, shortest trees.

A total of 100 trees were produced.

Terminology used in this paper follows Huys and Boxshall (1991). Type specimens have been deposited in the Kitakyushu Museum of Natural History and Human History (KMNH IvR).



**Fig. 2.** *Umazuracola elongatus* n. g., n. sp., female (A–E, paratype; F, G, holotype). **A**, rostrum and antennule, dorsal. **B**, mandible. **C**, maxillule. **D**, maxilla. **E**, leg 1, anterior. **F**, leg 2 and intercoxal plate, anterior. **G**, endopod of leg 2, anterior. Scales in millimeters.

## RESULTS

## Taxonomy

Order Poecilostomatoida Thorell, 1859

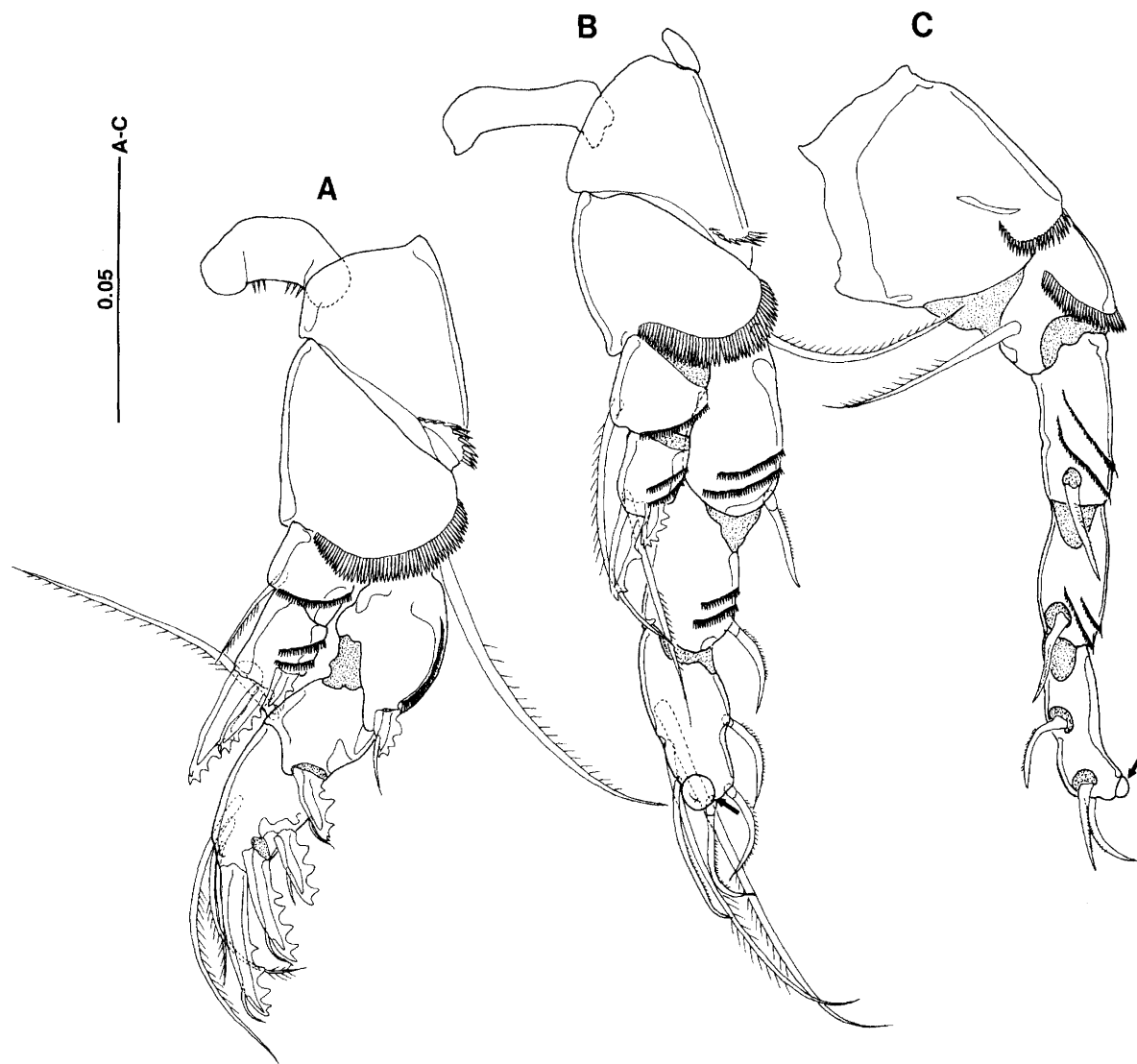
Umazuracolidae n. fam.

*Umazuracola* n. gen.

**Female.** Body elongated and slightly laterally compressed. Rostrum linguiform. Cephalosome fused with first pediger; third and fourth pedigers coalescent; somites of urosome also fused. Paired genital apertures located dorso-laterally at two-thirds length of urosome. Caudal ramus with 6 setae plus rudimentary seta 1. Antennule 7-segmented; formula of armature 5, 15, 5, 3, 4, 2 + aesthetasc, and 7 + aesthetasc. Antenna 3-segmented; endopod 2-segmented; second endopodal segment reflexed against proximal segment, furnished with pectinate, lamelliform plate. Mandible with 1 terminal and 1 subterminal blade. Maxillule represented by simple lobe tipped with 4 setae. Maxilla 2-segmented, consisting of unarmed, broad syncoxa and basis drawn out into serrate, spatulate process. Maxilliped indis-

tinctly 3-segmented; syncoxa robust and unarmed; basis narrow, with rudimentary distal seta; endopod tiny, drawn out into short spiniform process. Leg 1 biramous and reduced; protopod with outer distal seta; setal formula of exopod 1-0; 2,1,2; endopod 1-segmented and tipped with 3 setae. Legs 2 to 4 with 3-segmented exopod and 2-segmented endopod; both rami of legs 2 and 3 and endopod of leg 4 bearing stout, serrate spines. Leg 5 uniramous; protopod with outer seta; free exopodal segment with 2 outer and 2 terminal setae. Leg 6 represented by genital operculum armed with 1 spine and 2 setae. Egg-sac uniseriate.

**Male.** Body similar to but smaller than that of female. Paired genital opercula located ventrolaterally at midlength of urosome. Antennule, antenna, mandible, maxillule, and maxilla and legs 1-3 similar to those of female. Maxilliped well developed as grasping organ, 4-segmented. Legs 3 and 4 alike, with exopodal segments bearing stout, serrate spines; segmentation and setation of leg 5 as in female, but free exopodal segment much longer than protopodal segment; leg 6 represented by unarmed genital operculum.



**Fig. 3.** *Umazuracola elongatus* n. g., n. sp., female (A, B, holotype; C, paratype). **A**, leg 3 and intercoxal plate, anterior. **B**, leg 4 and intercoxal plate, anterior, round knob on third exopodal segment arrowed. **C**, leg 4, lateral, round knob on third exopodal segment arrowed. Scale in millimeters.

*Type-species.* *Umazuracola elongatus* n. sp.

*Etymology.* The generic name is a combination of *Uma-zura* (the common name of the host in Japanese, meaning "horse face") and *cola* (Latin, meaning "dweller, inhabitant"). Gender masculine.

*Umazuracola elongatus* n. sp.

(Figs. 1–6)

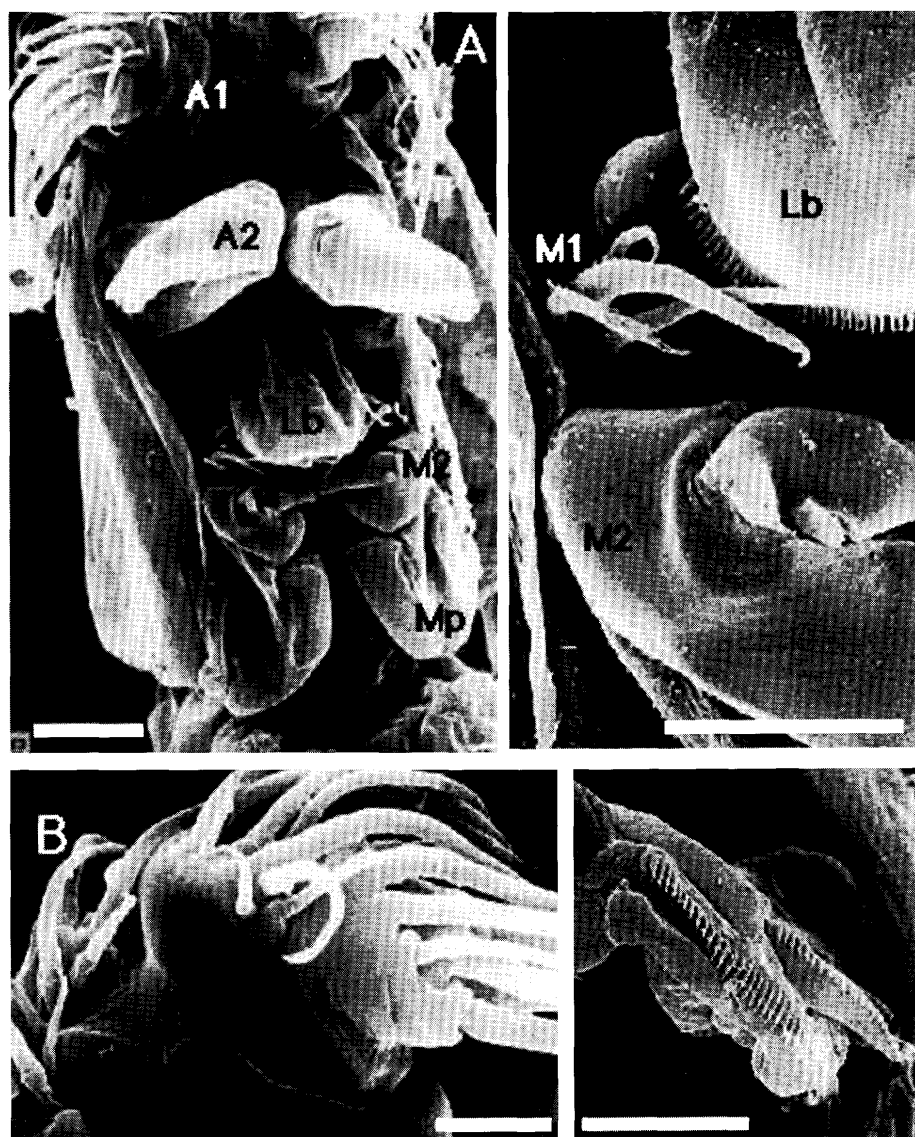
*Material examined.* Eighteen ♀♀ and 4 ♂♂ from body surface of 3 black scrapers, *Thamnaconus modestus* (Günther), caught in the Seto Inland Sea, western Japan, and purchased at a fish market at Imabari City in Ehime Prefecture on Shikoku Island: 5 ♀♀ and 2 ♂♂ from host 1 (236 mm in total length) purchased on 1 August 2003; 4 ♀♀ and 2 ♂♂ from host 2 (290 mm in total length) purchased on 9 May 2005; 9 ♀♀ from host 3 (300 mm in total length) purchased on 9 May 2005.

*Types.* Holotype (KMNH IvR 500, 126): 1 ♀, intact specimen, collected from host 1. Paratypes: 4 ♀♀ (2 intact, another 2 dissected and mounted on glass slides) and 2 ♂♂

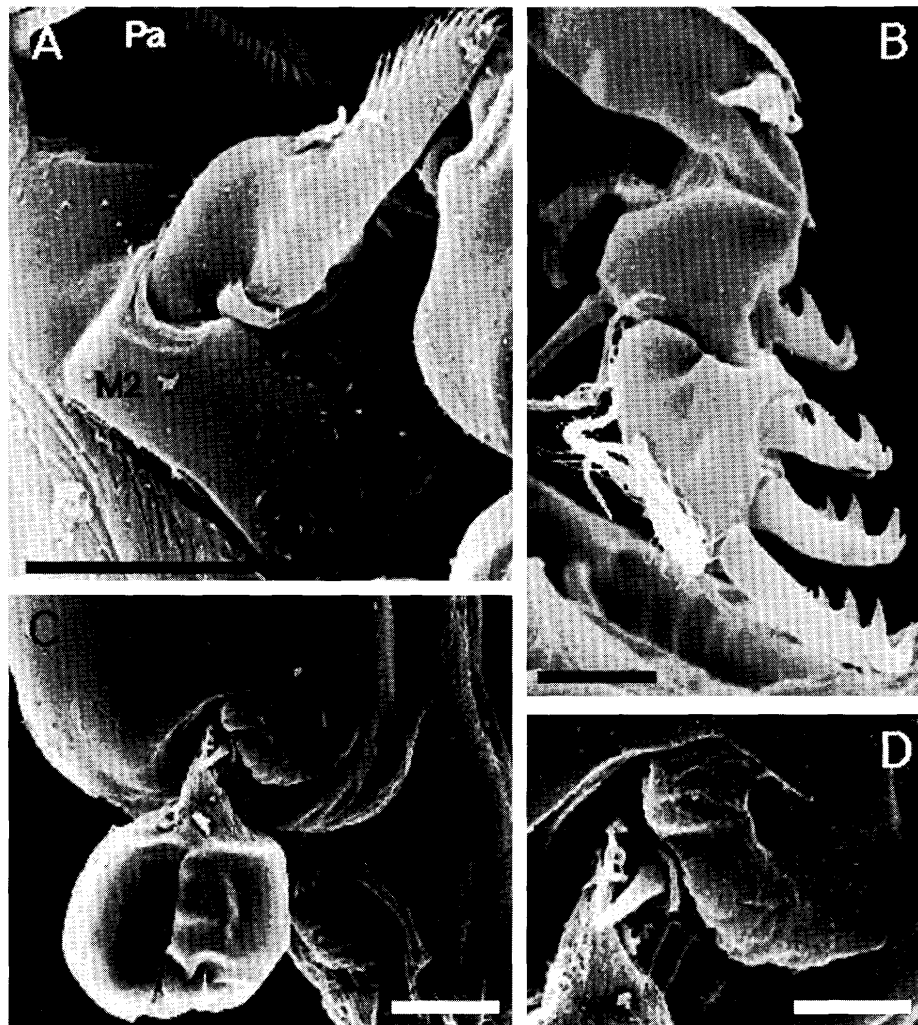
(whole specimens) collected from host 1 (KMNH IvR 500, 127/132); 4 ♀♀ (whole specimens) and 12 ♂♂ (dissected and mounted on a glass slide) collected from host 2 (KMNH IvR 500, 133–138); and 9 ♀♀ (intact specimens) collected from host 3 (KMNH IvR 500, 139–147).

*Body length.* Female: 0.95–1.29 mm (mean±standard deviation  $1.07\pm0.11$  mm,  $N=15$ ), excluding setae on caudal rami; holotype length, 1.03 mm. Male: 0.78–0.85 mm ( $0.81\pm0.03$  mm,  $N=4$ ).

*Female.* Body (Fig. 1A, B) elongated and slightly laterally compressed. Rostrum (Figs. 1A, 2A) linguiform, clearly demarcated from cephalosome. Cephalothorax (Fig. 1A, B; see Fig. 4A) consisting of cephalosome and first pediger, about 1.8 times as long as wide. Third and fourth pedigers also fused together, with fusion line clearly visible. Somites of urosome fused into one and clearly demarcated from prosome, with dorsally protruded genital area and gradually tapered abdomen (Fig. 1B). Paired genital apertures (Fig. 1B, C; see Fig. 5C, D) located dorsolaterally at two-thirds length of urosome; numerous glandular pores present ante-



**Fig. 4.** SEM micrographs of *Umazuracola elongatus* n. g., n. sp., female. **A**, cephalothorax, ventral. **B**, proximal segments of left antennule, ventral. **C**, distal (endopodal) segment of antenna. **D**, labrum, maxillule and maxilla, ventral. Abbreviations: A1=antennule, A2=antenna, Lb=labrum, M1=maxillule, M2=maxilla, Mp=maxilliped. Scales: 0.02 mm in A; 0.01 mm in B–D.



**Fig. 5.** SEM micrographs of *Umazuracola elongatus* n. g., n. sp., female. **A**, paragnath and maxilla. **B**, exopod of leg 3, anterior. **C**, genital area. **D**, leg 6. Abbreviations: M2=maxilla, Pa=paragnath. Scales: 0.01 mm in A, B, D; 0.02 mm in C.

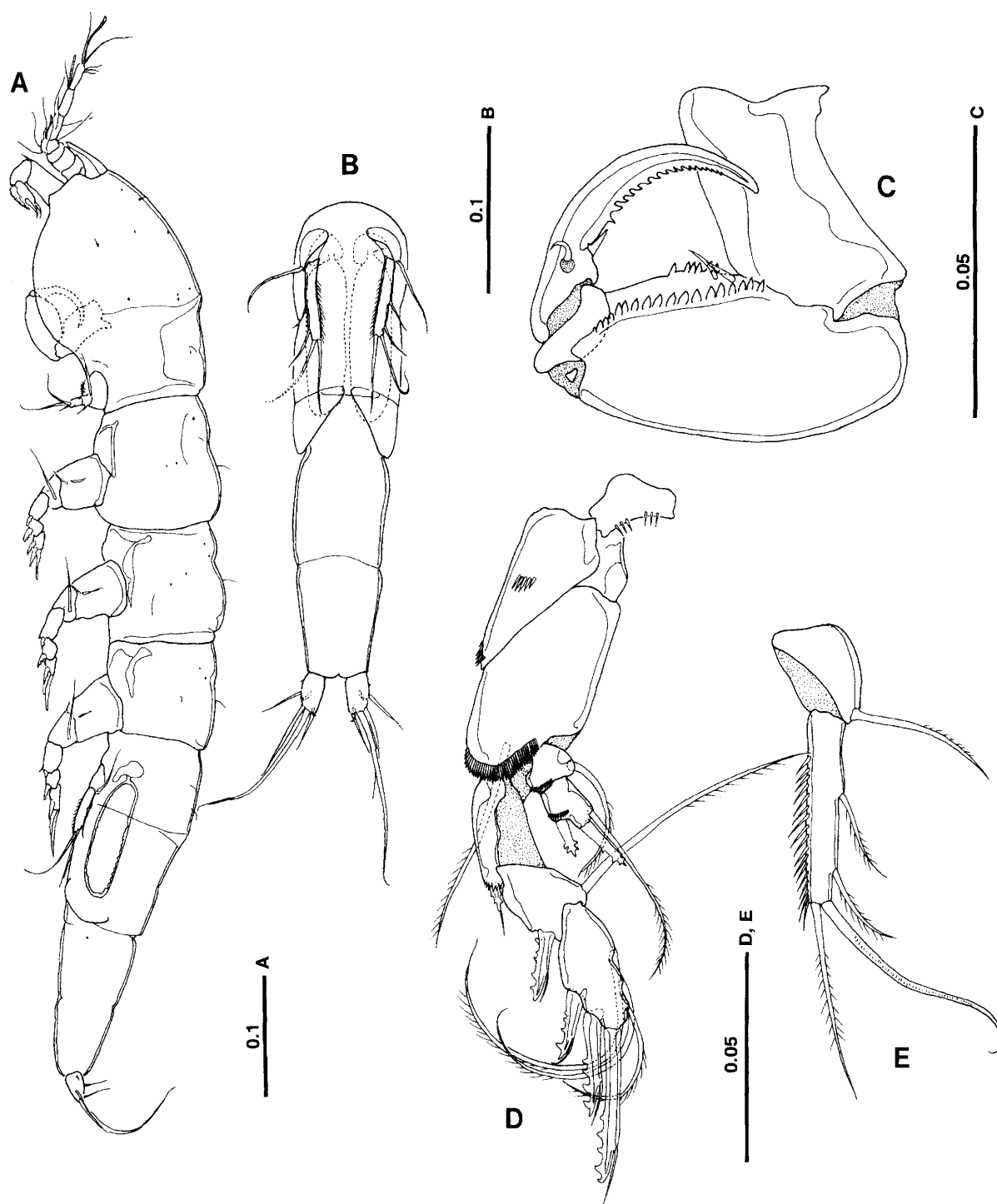
rior to genital aperture. Caudal ramus (Fig. 1E) ca. 1.4 times as long as wide, armed with 6 short and 1 (seta V) long setae; seta I rudimentary; seta II and VII located dorsally. Egg sac (Fig. 1D) uniseriate, carrying up to 16 eggs.

Antennule (Fig. 2A) 7-segmented, proximal two segments short, broad, and heavily sclerotized (see Fig. 4A, B); setal formula 5, 15, 5, 3, 4, 2 + ae, and 7 + ae. Antenna (Fig. 1G, H) 3-segmented, consisting of coxobasis and 2-segmented endopod; proximal segment with rudimentary seta terminally; middle segment with medial seta in midlength. Terminal segment reflexed against middle segment (see Fig. 4A), with long pectinate lamella on ventral margin; armature on this segment including subterminally 1 pectinate process (see Fig. 4A) and 1 hooked spine, and terminally 3 hooked spines and 2 naked setae (Fig. 1H; see Fig. 4C). Labrum (Fig. 1F; see Fig. 4A, D) protruding ventrally, concave posterior margin fringed with row of spinules (Fig. 1F; see Fig. 4D). Mandible (Figs. 1F, 2B) with 1 subterminal and 1 terminal toothed blade. Paragnath (Fig. 1F) lobate, with terminal row of setules (see Fig. 5A). Maxillule (Figs. 1F, 2C) represented by small lobe tipped with 4 setae, one of which pinnate on one side (see Fig. 4D). Maxilla (Figs. 1F, 2D) 2-segmented; broad syncoxa unarmed; basis drawn out into serrate process with short spiniform seta on outer

margin (see Figs. 4A, D, 5A). Maxilliped (Fig. 1F; see Fig. 4A) highly reduced and indistinctly 3-segmented; syncoxa broad, unarmed; basis bearing rudimentary terminal seta; endopod drawn out into slender spiniform process tapering distally. Legs 1–4 biramous, with 3-segmented exopod and 2-segmented endopod, except leg 1. Armature of these legs as follows (Roman numerals indicating spines and Arabic numerals, setae):

	Coxa	Basis	Exopod	Endopod
Leg 1	0–0	1–0	1–0; 2,1,2	1,1,1
Leg 2	0–0	1–0	1–0; 1–1; II,I,3	0–1; I,II,2
Leg 3	0–0	1–0	1–0; 1–1; II,I,3	0–1; I,II,0
Leg 4	0–0	1–0	1–0; 1–0; 2,1,3	0–1; I,I,1

Leg 1 (Fig. 2E) highly reduced, coxa and basis completely fused and bearing long outer, basal seta; intercoxal plate broad, furnished with row of setules along outer distal and central margins. Leg 2 (Fig. 2F) with row of spinules on outer distal corner of coxa; basis shorter than coxa, bearing long outer seta and transverse row of spinules along distal margin; intercoxal plate narrow. First exopodal segment with row of tightly arranged spinules along outer margin; all outer spines strongly serrate and carrying minute medial setule



**Fig. 6.** *Umazuracola elongatus* n. g., n. sp., male (paratype). **A**, habitus, lateral. **B**, urosome, ventral. **C**, maxilliped. **D**, leg 4, anterior. **E**, leg 5, anterior. Scales in millimeters.

(see Fig. 5B). Endopod about half as long as exopod; first segment with 1 and second segment with 2 oblique rows of tightly arranged spinules on anterior surface (Fig. 2G). Left endopod of leg 2 on holotype aberrant, its second segment shorter than that in normal right leg and bearing single terminal spine. Leg 3 (Fig. 3A) resembling leg 2 in segmentation, ornamentation, and armature, but no seta on second endopodal segment; intercoxal plate wider than long. Proto-pod of leg 4 (Fig. 3B) as in legs 2 and 3, but exopod prolonged; each of first two segments with two rows of minute spinules and one spiniform seta, third segment bearing

round terminal knob (arrowed in Fig. 3B, C), and 1 terminal and 2 outer spiniform setae and 3 inner pinnate setae; endopod one-third as long as exopod; proximal segment with 1 and distal segment with 2 oblique rows of tightly arranged spinules. Leg 5 (Fig. 1B, I) rudimentary and uniramous; proto-pod with outer seta; exopod 1-segmented and carrying 2 outer and 2 terminal setae. Leg 6 (Fig. 1C; see Fig. 5C, D) represented by 1 spine and 2 setae located on genital operculum.

*Male.* Body (Fig. 6A) similar to but smaller than that of female. Urosome (Fig. 6B) incompletely 3-segmented; fifth

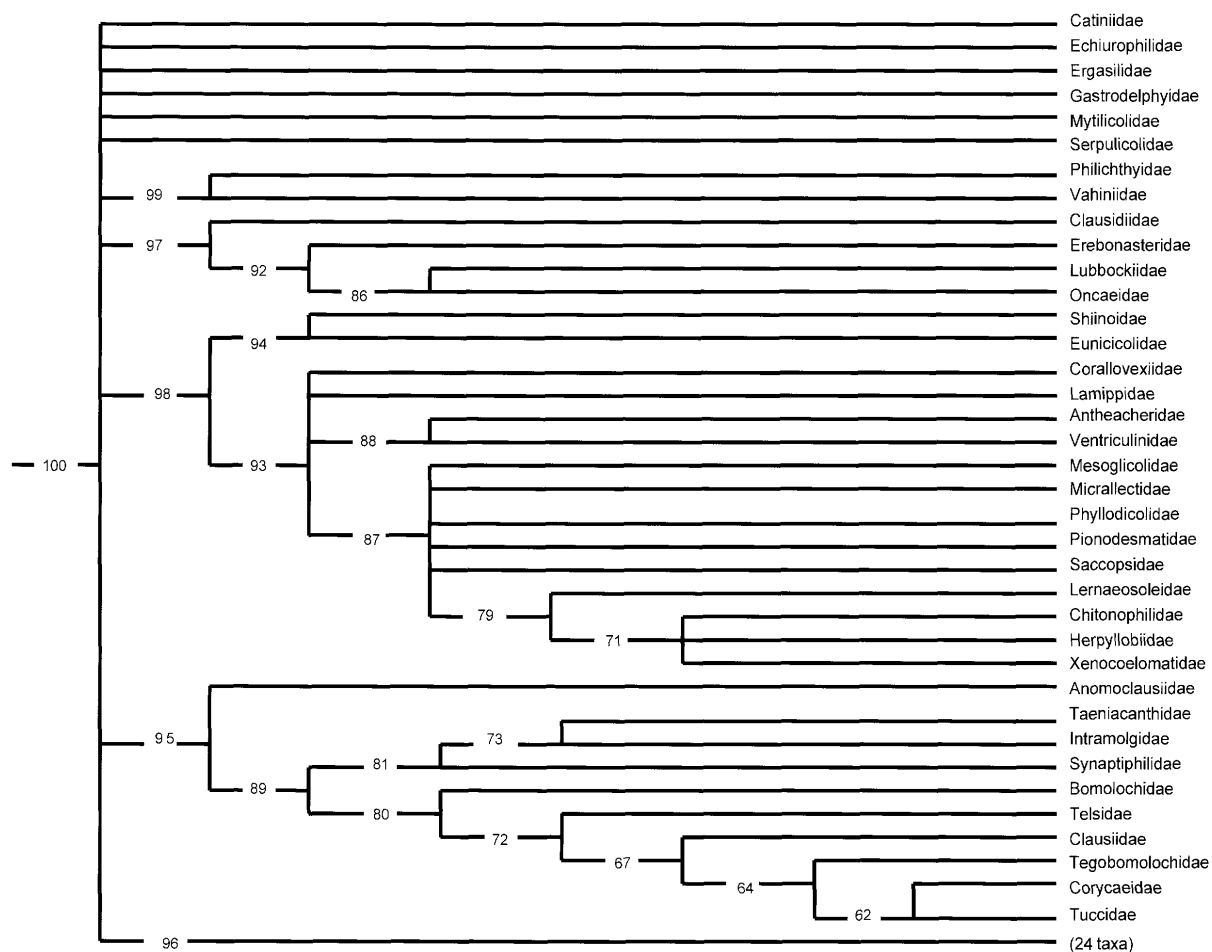


Fig. 7. Cladogram of Poecilostomatoida produced through analysis of 138 morphological characters. Clade 96 is shown in Fig. 8.

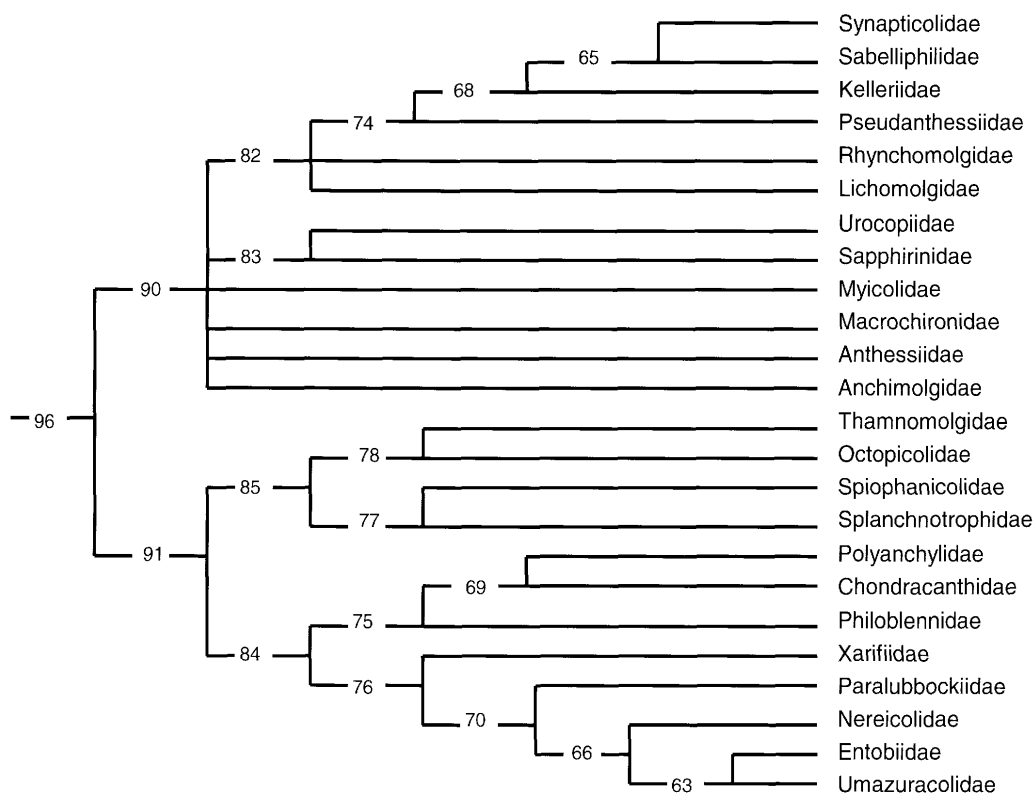


Fig. 8. Partial cladogram of Poecilostomatoida showing clade 96 (see Fig. 7 for position of clade).



pediger fused to genital somite, with suture clearly visible dorsally and laterally; genital somite with paired genital flaps; paired spermatophores in anterior part of urosome; abdomen 1-segmented, tapering distally, with constriction midway. Caudal rami as in female.

Antennule, antenna, mandible, maxillule, and maxilla as in female. Maxilliped (Fig. 6C) highly developed, 4-segmented; first segment (syncoxa) robust, unarmed; second segment (basis) expanded midway, with two rows of blunt teeth along medial margin and 2 short, basal setae; third segment (first endopodal segment) small, unarmed; fourth segment (second endopodal segment) drawn out into smoothly curved claw with 2 short, basal setae and serration along medial margin.

Legs 1 to 3 similar to those of female. Leg 4 (Fig. 6D) with spines (instead of setae) on exopod bearing teeth only on outer margin; no round knob on third exopodal segment; intercoxal sclerite with rows of spinules along posterior margin. Leg 5 (Fig. 6B, E) 2-segmented, free exopodal segment much longer than protopodal segment and with row of spinules along inner margin. Leg 6 (Fig. 6B) represented by unarmed genital flap.

**Etymology.** The specific name "*elongatus*" is from Latin, meaning "elongate," alluding to the elongated body in this new species.

### Phylogenetic analysis

A cladistic analysis was undertaken to elucidate the phylogenetic relationships of the new family with the other 60 families in the Poecilostomatoida. The analysis produced 100 trees with a length of 560 steps, consistency index (CI) of 0.24, and retention index (RI) of 0.74. Since the purpose of this analysis was to investigate phylogenetic relationships among families, the special command "Nelsen" in HENNIG86 was used to construct a strict consensus tree for the 100 trees obtained. This strict consensus tree is reproduced in Fig. 7, with the topography of one of its branches, clade 96, given separately in Fig. 8. The synapomorphies on the 39 nodes (62 to 100) of this tree are listed in Appendix 3.

### DISCUSSION

Having an antenna armed with a claw on the second endopodal segment, a mandible with 2 distal blades, a maxillule tipped with 4 elements, and a maxilla with a spinulose terminal process, *Umazuracola elongatus* resembles a group of poecilostomatoid families called the "bomolochiform complex" (Dojiri and Cressey, 1987; Ho, 1991; Boxshall and Halsey, 2004). The complex, comprising the families Bomolochidae, Taeniacanthidae, Tegobomolochidae, Telsidae, and Tuccidae, was characterized by Dojiri and Cressey (1987) as sharing the following five characters: (1) indistinctly 4-segmented antenna with two pectinate processes, claw-like spines, and setae; (2) mandible with two subequal spinulated blades; (3) maxilla bearing spinulose elements; (4) an indented (concave) ventral surface of the cephalothorax; and (5) lamelliform leg 1. The family Telsidae differs from the other four families in the complex in having a cephalothorax without concave ventral surface and an unmodified (not lamelliform) leg 1 (Ho, 1967); *U. elongatus* also shows these differences. However, the maxilliped and the four pairs of legs on *U. elongatus* are so different from those

of the Telsidae that it cannot be placed in the latter family. Thus, we proposed a new family to accommodate *U. elongatus*.

Sixty-one families of copepods are currently known in the order Poecilostomatoida. The family Pharodidae Illg, 1948, one of the 61 families listed in Poecilostomatoida by Martin and Davis (2001), was recently synonymized with Chondracanthidae Milne Edwards, 1840 by Østergaard *et al.* (2003). Additionally, another family, Nucellicolidae Lamb, Boxshall, Mill, and Grahame, 1996, was relegated as a synonym of Chitonophilidae Avdeev and Sirenko, 1991 by Boxshall and Halsey (2004). However, with the resurrection of a forgotten poecilostomatoid family, Pionodesmotidae Bonnier, 1898 – containing endoparasites of sea urchins – by Boxshall and Halsey (2004) and our addition of a new family, the number of poecilostomatoid families remains 61, as stated in MATERIALS AND METHODS.

It is interesting that in Ho's (1991) original analysis of the Poecilostomatoida, the families Corycaeidae and Clausiidae appeared in monophyly with the five families of the bomolochiform complex. These families again appeared in the same clade (clade 89) in our analysis (see Fig. 7), and share as synapomorphies characters 17 (antenna with claw on penultimate segment) and 22 (mandible a process with 3 terminal elements). Also, eight (Anchimolgidae, Kellieridae, Lichomolgidae, Macrochironidae, Pseudanthessiidae, Rhynchomolgidae, Sabelliphilidae, and Synapticolidae) of the ten (plus Octopicolidae and Thamnomolgidae) families of the "lichomolgoid complex" recognized by Humes and Boxshall (1996) comprise a monophyletic group (clade 90; see Fig. 8) containing also four other families (Anthessiidae, Mycolidae, Sapphirinidae, and Urocopiidae). The synapomorphies for this clade are characters 25 (mandible lash-like), 31 (maxillule unilobate with 4 elements), and 110 (terminal segment of leg 4 exopod with 9 elements).

Much to our surprise, our parsimony analysis showed the new family Umazuracolidae not to be a member of the bomolochiform complex, despite its resemblance to the latter in the structure of the antenna, mandible, maxillule, and maxilla. Examination of the list of the synapomorphies for node 95 (Appendix 3) indicated that Umazuracolidae is excluded from the bomolochiform complex (clade 95 in Fig. 8) chiefly by lacking character 43 (maxilliped endopod a claw), reversal of character 66 (leg 1 basis without medial seta), and absence of character 125 (middle endopodal segment of leg 4 with 1 medial seta). Umazuracolidae is the sister-taxon to a polychaete-parasitizing family, Entobiidae Ho, 1984, sharing characters 28 (bilobate maxillule), 64 (1-segmented leg 1 endopod), and 133 (leg 5 reduced to a seta). It is interesting that the sister-taxon of Umazuracolidae + Entobiidae is another polychaete-parasitizing family, Nereicolidae Claus, 1875. This suggests that the fish-parasitizing *Umazuracola* has evolved from a copepod parasitic on polychaetes.

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**Appendix 1.** Apomorphic states of characters of the poecilostomatoid families used in the cladistic analysis.

CHARACTER	CHARACTER STATES	CHARACTER	CHARACTER STATES
1	First pediger separated from cephalosome	70	Leg 2 exopod 3 <sup>rd</sup> segment with 7 elements
2	Urosome (including caudal ramus) short, less than 1/3 of prosome	71	Leg 2 exopod 3 <sup>rd</sup> segment with 6 elements
3	Abdomen 4-segmented	72	Leg 2 exopod 3 <sup>rd</sup> segment with 4 elements
4	Abdomen 2-segmented	73	Leg 2 exopod 3 <sup>rd</sup> segment with 3 elements
5	Abdomen 1-segmented	74	Leg 2 exopod 3 <sup>rd</sup> segment without armature
6	Antennule 8-segmented	75	Leg 2 exopod 2-segmented
7	Antennule 7-segmented	76	Leg 2 exopod 1-segmented
8	Antennule 6-segmented	77	Leg 2 endopod 3 <sup>rd</sup> segment with 7 elements
9	Antennule 5-segmented	78	Leg 2 endopod 3 <sup>rd</sup> segment with 5 elements
10	Antennule 4-segmented	79	Leg 2 endopod 3 <sup>rd</sup> segment with 4 elements
11	Antennule 2-segmented	80	Leg 2 endopod 3 <sup>rd</sup> segment with 3 elements
12	Antennule 1-segmented	81	Leg 2 endopod 3 <sup>rd</sup> segment with 2 elements
13	Antennule absent	82	Leg 2 endopod 3 <sup>rd</sup> segment with 1 element
14	Antenna 3-segmented	83	Leg 2 endopod 3 <sup>rd</sup> segment without armature
15	Antenna 2-segmented	84	Leg 2 endopod 2-segmented
16	Antenna with claw(s) on terminal segment	85	Leg 2 endopod 1-segmented
17	Antenna with claw (s) on penultimate segment	86	Leg 2 endopod absent
18	Antenna modified into a uncinat appendage	87	Leg 2 endopod 2 <sup>nd</sup> segment with 1 medial seta
19	Antenna bomolochiform, with endopod folded back over coxobasis	88	Leg 2 endopod 2 <sup>nd</sup> segment without medial seta
20	Antenna absent	89	Leg 2 modified into a lobe
21	Mandible a process with 4 terminal elements	90	Leg 2 absent
22	Mandible a process with 3 terminal elements	91	Leg 3 exopod 3 <sup>rd</sup> segment with 8 elements
23	Mandible a process with 2 terminal elements	92	Leg 3 exopod 3 <sup>rd</sup> segment with 7 elements
24	Mandible a small blade	93	Leg 3 exopod 3 <sup>rd</sup> segment with 6 elements
25	Mandible lash-like	94	Leg 3 exopod 3 <sup>rd</sup> segment with 4 elements
26	Mandible a tapering blade	95	Leg 3 exopod 3 <sup>rd</sup> segment with 3 elements
27	Mandible absent	96	Leg 3 exopod 3 <sup>rd</sup> segment without armature
28	Maxillule bilobate	97	Leg 3 exopod 2-segmented
29	Maxillule unilobate with 6 elements	98	Leg 3 exopod 1-segmented
30	Maxillule unilobate with 5 elements	99	Leg 3 endopod 3 <sup>rd</sup> segment with 5 elements
31	Maxillule unilobate with 4 elements	100	Leg 3 endopod 3 <sup>rd</sup> segment with 4 elements
32	Maxillule unilobate with 3 elements	101	Leg 3 endopod 3 <sup>rd</sup> segment with 3 elements
33	Maxillule unilobate with 2 elements	102	Leg 3 endopod 3 <sup>rd</sup> segment with 2 elements
34	Maxillule absent	103	Leg 3 endopod 3 <sup>rd</sup> segment with 1 element
35	Maxilla basis with 4 elements	104	Leg 3 endopod 2-segmented
36	Maxilla basis with 3 elements	105	Leg 3 endopod 1-segmented
37	Maxilla basis with 2 elements	106	Leg 3 endopod absent
38	Maxilla basis with 1 element	107	Leg 3 endopod 2 <sup>nd</sup> segment with 1 medial seta
39	Maxilla basis unarmed	108	Leg 3 modified into a sac without seta
40	Maxilla absent	109	Leg 3 absent
41	Maxilliped with 2-segmented endopod	110	Leg 4 exopod 3 <sup>rd</sup> segment with 9 elements
42	Maxilliped endopod a pointed process	111	Leg 4 exopod 3 <sup>rd</sup> segment with 7 elements
43	Maxilliped endopod a claw	112	Leg 4 exopod 3 <sup>rd</sup> segment with 6 elements
44	Maxilliped endopod a spinulose lobe	113	Leg 4 exopod 3 <sup>rd</sup> segment with 5 elements
45	Maxilliped (2-segmented) endopod absent	114	Leg 4 exopod 3 <sup>rd</sup> segment with 3 elements
46	Maxilliped absent	115	Leg 4 exopod 3 <sup>rd</sup> segment without armature
47	Leg 1 exopod 3 <sup>rd</sup> segment with 9 elements	116	Leg 4 exopod 2-segmented
48	Leg 1 exopod 3 <sup>rd</sup> segment with 7 elements	117	Leg 4 exopod 1-segmented
49	Leg 1 exopod 3 <sup>rd</sup> segment with 6 elements	118	Leg 4 endopod 3 <sup>rd</sup> segment with 4 elements
50	Leg 1 exopod 3 <sup>rd</sup> segment with 5 elements	119	Leg 4 endopod 3 <sup>rd</sup> segment with 3 elements
51	Leg 1 exopod 3 <sup>rd</sup> segment with 4 elements	120	Leg 4 endopod 3 <sup>rd</sup> segment with 2 elements
52	Leg 1 exopod 3 <sup>rd</sup> segment with 3 elements	121	Leg 4 endopod 3 <sup>rd</sup> segment with 1 element
53	Leg 1 exopod 3 <sup>rd</sup> segment without armature	122	Leg 4 endopod 2-segmented
54	Leg 1 exopod 2-segmented	123	Leg 4 endopod 1-segmented
55	Leg 1 exopod 1-segmented	124	Leg 4 endopod absent
56	Leg 1 endopod 3 <sup>rd</sup> segment with 7 elements	125	Leg 4 endopod 2 <sup>nd</sup> segment with 1 medial seta
57	Leg 1 endopod 3 <sup>rd</sup> segment with 5 elements	126	Leg 4 modified into a sac without seta
58	Leg 1 endopod 3 <sup>rd</sup> segment with 4 elements	127	Leg 4 absent
59	Leg 1 endopod 3 <sup>rd</sup> segment with 3 elements	128	Leg 5 2-segmented, terminal segment with 4 elements
60	Leg 1 endopod 3 <sup>rd</sup> segment with 2 elements	129	Leg 5 2-segmented, terminal segment with 2 elements
61	Leg 1 endopod 3 <sup>rd</sup> segment with 1 elements	130	Leg 5 1-segmented and armed with 4 elements
62	Leg 1 endopod 3 <sup>rd</sup> segment without armature	131	Leg 5 1-segmented and armed with 3 elements
63	Leg 1 endopod 2-segmented	132	Leg 5 1-segmented and armed with 2 elements
64	Leg 1 endopod 1-segmented	131	Leg 5 1-segmented and armed with 3 elements
65	Leg 1 endopod absent	132	Leg 5 1-segmented and armed with 2 elements
66	Leg 1 basis without medial seta	133	Leg 5 reduced to a seta
67	Leg 1 modified into a lobe	134	Leg 5 absent
68	Leg 1 absent	135	Leg 6 represented by 4 setae on genital operculum
69	Leg 2 exopod 3 <sup>rd</sup> segment with 8 elements	136	Leg 6 represented by 2 setae on genital operculum
		137	Leg 6 represented by 1 seta on genital operculum
		138	Leg 6 absent

**Appendix 2.** Character matrix

Taxon (family)	Characters					
ANCHIM	0000001000	0000010000	0000100000	1000001000	0100000000	0000000000
	0000010000	0000000000	0000000000	0000000010	0000000001	0000000001
	0100?00000	01000100				
ANOMOC	0100001000	0000010000	0100000100	0000000100	0010000000	0100000000
	1010000000	0010000000	010100?000	0000100000	001100?000	0001000000
	1100?00100	00000010				
ANTHEA	1001000000	0011000000	000000?000	000?000010	0000100000	0011000000
	0110010000	0001100000	001100?000	0000000000	0000011010	0000000000
	0000001000	000?0001				
ANTHES	1000001000	0000010000	0010000000	1000001000	1000000000	0000000000
	0000010000	0000000000	0000000000	0000000000	0000000001	0000000000
	0000000001	00000100				
BOMOLO	0000010000	0000011010	0100000001	0000001000	0010000000	0000000000
	0000000000	0000000100	0000000000	0000000001	0000000001	0000000010
	0000100100	00000000				
CATINI	0000000100	0000000000	1000000001	0000100000	0000010100	0000000000
	0000000001	0000000000	0000001000	1000000000	0000001000	0000000100
	0000100100	00000000				
CHITON	0000?00000	0010000001	0000001000	0001000001	0000010000	0000000000
	0000110100	0000000000	0000011001	0000000000	0000011010	0000000000
	0001001000	00010001				
CHONDR	1101000100	0000101100	0000010000	0100000001	0000010000	0000000000
	0000110110	0000100000	000100?000	0010001000	010100?000	0000000000
	0001001000	10000100				
CLAUSD	0010001000	0000000000	0000000100	0000010000	1000000000	0000000000
	0000000000	0000000000	0000000000	0000000000	0000000001	0000000000
	0000000100	00000000				
CLAUSI	0010000100	0000011000	0010000000	1000001000	1000000100	0000001000
	0000000000	0000000000	0000000000	0000000000	0000000001	0000000100
	0000000100	00000100				
CORALL	1000?00000	1001010000	0000001000	000?00000?	00000?0000	0000000000
	0000001000	0000000000	0000000010	0000000000	0000011010	0000000000
	0001001000	00010001				
CORYCA	0000100100	0000011000	1000000100	0000010000	0010000000	0000001000
	0000010000	0000000010	0000000000	0000000000	0100000000	1000000001
	0010000000	00100010				
ECHIUR	0000000100	0000011000	0001000000	0100000100	0000010010	0000001000
	0000000000	1000000100	0000001000	0010000001	0000001000	0100000010
	0000500100	00000001				
ENTOBI	1000500000	1001000000	0010000000	1000000001	0010000000	00???00000
	0???010000	000???0000	00???0?000	00000???00	000?0?0000	0000???000
	0???0?0000	00100001				
EREBON	1000001000	0000000000	1000000100	0000001000	1000000000	0000000000
	0000000000	0000000000	0000000000	0000000000	0000000000	0000000000
	0000000100	00000100				
ERGASI	0100000100	0000010000	0100000000	0100000100	0000010100	0000000000
	0000010001	0000000100	0000000000	0100000010	0000000000	0010010100
	0000000010	00000001				
EUNICI	0000001000	0001010000	1000000000	0100001000	0100000001	0000000001
	0010010000	1000000001	000100?000	0000101000	0000010000	0000000000
	0001001000	00010001				
GASTRO	1100000010	0000010000	0010000000	0100000010	0000010100	0000001000
	0000010010	0000000100	0000000000	0010000000	1000000000	0000000000
	0000010000	00010100				
HERPYL	0100?00000	0010000001	0000001000	0001000001	0000010000	0000000000
	0000110100	0000000000	000001?001	0000000000	000001?010	0000000000
	0001001000	00010001				
INTRAM	0100001000	0000011000	0000000010	0000010000	0010000100	0000000000
	0000010010	0000000000	0000000000	1000000000	0000000000	0000000100
	0000000000	00100000				
KELLER	1000001000	0000011000	0000100000	1000010000	0000000000	0000000000
	0000010000	0000000000	0000000000	0000000010	0000000000	0000000010
	0010?00000	01000100				
LAMMIP	0001000010	0000010000	0000001000	0001000001	0010000000	0101000001
	0001010000	0010100000	100010?000	0000000000	0000010010	0000000000
	0001001000	00010001				
LERNAE	0100?00000	0100000100	0000001000	0001000001	0000010000	0000000000
	0000?11000	0000000000	0000011001	0000000000	0000011010	0000000000
	0001101000	00010001				
LICHOM	0000001000	0000010000	0000100000	1000010000	0100000000	0000000000
	0000010000	0000000000	0000000000	0000000000	0000000001	0000000010
	0000100000	01000100				
LUBBOC	1000001000	0000010000	1000000100	0000100000	1010000000	0000000000
	0000000000	0000000000	0000000000	1000000000	0000000000	0000000000
	0000000000	01000100				
MACROC	1000001000	0000001000	0000100000	1000001000	0010000000	0000000000
	0000010000	0000000000	0000000000	0000000010	0000000001	0000000001
	0010?00000	01000100				
MESOGL	1010000000	1001011000	0000001000	0001000010	00000?0000	0000000000
	0000110100	0000000000	0000010001	0000000000	0000010010	0000000000
	0001001000	00010001				
MICRAL	0100?00000	1001000000	0100000000	10000000?0	0001000000	0000000000
	0000110100	0000000000	0000010001	0000000000	0000010010	0000000000
	0001001000	00010001				
MYICOL	0000001000	0001010000	1000000000	1000001000	00000?0000	0000000000
	0000000000	0000000000	0000000000	0000000000	0000000001	0000000000
	0000000100	00000100				
MYTILI	1101000000	0001010000	0000001000	0010000010	0000010000	0000000100
	0000010010	0000000000	0000000000	1000000001	0000000000	1000000010
	0000000001	00000100				

## New Family of Poecilostomatoid Copepods

495

NEREIC	1100101000 0?10010000 000?010000	0001010000 000?100000 00100100	0010000100 00?1000000 0000010000	0000000010 00000?1000 0000000000	0001000000 00010000000 0000000000	00?1000000 0000000000 0000000000
OCTOPI	1010001000 0000010000 0010000000	0000011000 0000000000 01000100	0000010000 0000000000 0000000000	0010001000 0000000010 0000000000	0100000000 0000000000 0000000000	0000000000 0000000010 0000000000
ONCAEI	1000001000 0000000000 0000000000	0001000000 0000000000 01000100	0000000100 0000000000 0000000000	0000000000 0000000010 0000000000	1000000000 0000000000 0000000000	0000000000 0000000000 0000000000
PARALU	1000001000 0010010001 0100?00000	0000100000 0000001000 01000100	0100000100 000100?000 0000000000	0000010000 0100000000 0000000000	1000000010 000100?000 0000000000	0000000000 1000000100 0000000000
PHILIC	1010010000 0101010000 000??10000	0000000001 0100100000 0000100	0000001000 001010?000 0000000000	1000100000 0000000000 0000000000	0000?00000 00000??100 0000000000	0101000000 0000000000 0000000000
PHILOB	0000000100 0010010000 0001001000	0001010000 1000000100 01000100	0000010000 000100?000 0000000000	1000010000 0000000000 0000000000	0100000010 00000?0100 0000000000	0000000000 0000000000 0000000000
PHYLLLO	0000?00000 0000110100 0001001000	0100010000 0000000000 00010100	0000001000 0000010001 00010100	0001000001 0000000000 0000000000	0010000000 0000010010 0000000000	0000000000 0000000000 0000000000
PIONOD	1100100100 0000110100 0001001000	0000001000 0000000000 00010000?	000000?100 0000010001 0000000000	0000?00000 0000000000 0000000000	0010000000 0000010010 0000000000	0000000000 0000000000 0000000000
POLYAN	1000000100 0010010010 0001000000	0000110000 0000001000 010000010	0000010000 000100?000 0000000000	1000001000 1000000000 0000000000	0010000100 000100?000 0000000000	0000010000 0010001000 0000000000
PSEUDA	1000001000 0000010000 0100?00000	0000010000 0000000000 00100100	0000100000 0000000000 0000000000	1000010000 0000000000 0000000000	0100000000 0000000000 0000000000	0000000000 0000000000 0000000000
RHYNCH	1000001000 0000010000 0000000000	0000010000 0000000000 01000100	0000100000 0000000000 0000000000	1000010000 0000000000 0000000000	0100000000 0000000001 0000000000	0000000000 0000000000 0000000000
SABELL	1000001000 0000010000 0000100000	0000011000 0000000000 01000100	0000010000 0000000000 0000000000	1000010000 0000000000 0000000000	0010000000 0000000000 0000000000	0000000000 0000000000 0000000000
SACOP	1100?00100 0000110100 0001001000	0000100000 0000000000 00010001	0000001000 0000010001 0000000000	000100?000 0000000000 0000000000	0000010000 0000010010 0000000000	0000000000 0000000000 0000000000
SAPPHI	0000000100 0000010000 0000100000	0000001000 0000000000 01000100	0000010000 0000000000 0000000000	1000001000 0000000010 0000000000	0010000000 0000000000 0000000000	0000000000 0000000000 0000000000
SERPUL	1000?00100 0000000010 0000100001	0000000000 0000000001 00001000	0000010000 0000001000 0000000000	0100001000 1000000000 0000000000	0001000010 1000001000 0000000000	0000000100 0000000010 0000000000
SHIINO	0000001000 0000010000 0001001000	0000101000 1000000001 00010100	0010000000 0000000100 00010100	0100001000 0000000000 0000000000	0000010010 0000000100 0000000000	0000000010 0000000000 0000000000
SPIOPH	1000100100 0001010000 0010?00000	0000000000 0001010001 01000001	0000010000 000010?000 0000000000	0010000100 0000010100 0000000000	1010000000 100010?000 0000000000	0010100100 0000101001 0000000000
SPLANC	1001000001 0101010000 0001001000	0001010000 0001010000 01000100	0000010000 001010?000 0000000000	0010000100 0000000000 0000000000	0000010000 0000000100 0000000000	0010100000 0000000000 0000000000
SYNAPC	1000001000 0000010000 0000000000	0000001000 0000000000 01000100	0000010000 0000000000 0000000000	1000010000 0000000000 0000000000	0100000000 0000000000 0000000000	0000000000 0000000000 0000000000
SYNAPP	0000010000 0000000000 0100?00100	0000001000 0000000000 0000000?	0100000000 0000000000 0000000000	1000010000 0000000000 0000000000	0000100000 0000000000 0000000000	0000000000 0000000000 0000000000
TAENIA	0010001000 0000000000 0000100100	0000011010 0000000000 00000000	0100000010 0000000000 0000000000	0000010000 1000000000 0000000000	0010000000 0000000000 0000000000	0000000000 0000000100 0000000000
TEGOBO	0000000100 0000010001 0000000100	0000011010 0000000100 00000001	0010000000 0000000000 0000000000	1000010000 0100000000 0000000000	0010001000 1000000000 0000000000	0001001000 1000000010 0000000000
TELSID	0000000100 0000000000 0000100100	0000011010 0000000000 00000000	0010000000 0000000000 0000000000	1000000010 1000000001 0000000000	0010000000 0000000000 0000000000	0000000000 0010000010 0000000000
THAMNO	1000001000 0000010000 1010?00000	0000010000 0000000000 01000100	0000010000 0000000000 0000000000	0010000100 0000000000 0000000000	0000000000 001010?000 0000000000	0000000000 0000010000 0000000000
TUCCID	0100?00010 0000000000 1010?00000	0000011010 0000001000 10000001	0010000000 000100?000 0000000000	1000010000 0000000000 0000000000	0010000100 001010?000 0000000000	0000001000 0000010000 0000000000
UMAZUR	0000?01000 0001010000 0100?00001	0001011010 1000000000 00000000	0010000000 000100?000 0000000000	1000000100 0010000000 0000000000	0100000001 100100?000 0000000000	0001000010 0100000010 0000000000
UROCOF	1000000100 0000010000 0000100000	0000010000 0000000000 00100000	0000100000 0000000000 0000000000	1000000100 0000000000 0000000000	0010000000 0000000000 0000000000	0000000000 0000000000 0000000001
VAHINI	0000000001 0001010000 0000000000	0000010000 0010100000 00100100	0000010000 010010?000 0000000000	0000000100 0000000000 0000000000	0000100000 0000000100 0000000000	1001000001 0000000000 0000000000
VENTRI	0000000001 0?10010000 0001001000	0001010000 000?100000 00010001	0000010000 0000010000 0000010000	0010000010 0000000000 0000000000	0000010000 0000010010 0000000000	00?1000000 0000000000 0000000000
XARIFI	1000001000 0010010000 1100?00000	0000010000 0100000001 01000101	0000010000 000100?000 0000000000	0100000100 0001000000 0000000000	0001000000 001100?000 0000000000	1000000010 0001000000 0000000000
XENOCO	0100?00000 0000110100 0001?01000	0010000001 0000000000 00010001	0000001000 000001?001 0000000000	0001000001 0000000000 0000000000	0000010000 000001?010 0000000000	0000000000 0000000000 0000000000

**Appendix 3.** List of synapomorphies for the 39 nodes (clades) in Figs. 7 and 8. Underlined figures indicate reversal.

NODE		SYNAPOMORPHY							
100	016	066							
99	136								
98	106	124	127	134	138				
97	007	<u>016</u>	028	041	<u>066</u>				
96	001	007	037	132	<u>136</u>				
95	043	<u>066</u>	125						
94	032	037	071	080					
93	027	034	109						
92	001	021	136						
91	026								
90	025	031	110						
89	017	022							
88	014	039	053	054	062	063	074	075	
87	002	<u>016</u>	065	068	086	090			
86	132								
85	033								
84	063	084	104						
83	<u>007</u>	008	043	<u>110</u>	120				
82	036	<u>037</u>	042						
81	036	118							
80	019	100	119						
79	040	046	107						
78	042								
77	<u>007</u>	053	055	064	074	076	085		
76	122								
75	<u>007</u>	008	031	124	127				
74	<u>110</u>								
73	029	091							
72	008	<u>022</u>	023						
71	020	087							
70	<u>026</u>	028	<u>037</u>						
69	017	043	069						
68	017								
67	057	<u>100</u>	111	<u>125</u>					
66	005	014	023	054	<u>132</u>				
65	<u>025</u>	026							
64	036	066	138						
63	<u>028</u>	064	133	<u>136</u>					
62	005	<u>119</u>	123						